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Lower limb skeletal biomechanics track long-term decline in mobility across ~6150 years of agriculture in Central Europe[☆]

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A B S T R A C T

Central Europe is a region with a rich agricultural history that dates back to the emergence of the first Neolithic cultures here during the second part of the 6th millennium BC. The effects of prolonged cultural change on the skeletal morphology of agricultural populations in this region have not yet been fully reported. This study investigates diachronic trends in lower limb cross-sectional geometry among preindustrial Central Europeans spanning over 6000 years from the initial spread of agriculture in the region (~5300 cal BC) to the Early Medieval (~850 AD). Midshaft diaphyseal cross-sectional geometric (CSG) properties were derived from 443 three-dimensional laser scans of femora and tibiae. Results documented temporal change that was particularly pronounced in the tibia relative to the femur, indicative of declining compressional strength (males), bending and torsional rigidity (males), and increasingly more circular cross-sections (both sexes). When examined chronologically by cemetery, a major shift towards lower tibial rigidity was identified in the Late Bronze Age among males, after which time sexual dimorphism also declined. Regional variation in tibial rigidity was identified among males, being consistently low in males from modern-day Vojvodina (Serbia) relative to contemporaneous males elsewhere in Central Europe. In contrast, female temporal trends by cemetery were indicative of progressive but gradual declines in tibial loading. Results report systematic change in lower limb cross-sectional geometry among preindustrial Central European agriculturalists that are likely indicative of declining terrestrial mobility through 6000+ years of cultural change in the region.

The adoption of agriculture marked a fundamental shift, not just in human subsistence and diet, but in many aspects of culture, demography, and behavior as well. In preindustrial Europe, the persistent pace of socioeconomic and technological advancement following the introduction of agriculture should have provided the driving force for change in habitual behaviors and mobility patterns among men and women. The agricultural history of Central Europe is particularly rich, owing to its fertile loess soils and the density and diversity of its cultures, yet the characterization of long-term trends in lower limb morphology among agriculturalists in the region have only been undertaken quite recently. There is some indication that change in lower limb bone robusticity among Central European Late Eneolithic (Copper Age; Bell Beaker and Corded Ware) and Early Bronze Age (EBA; Únětice, Unterwölbling and Weiselburger) groups was gradual, suggesting similar mobility patterns in both Copper and Bronze Age groups in the region (Sládek et al., 2006a,b, 2007, 2012 (abstract)). However, the introduction of metallurgy, the increasing efficiency of agricultural and transportation technologies through time, and the increased trade and exchange that these all supported are likely to have affected more long-term trends in Central European limb loading, mobility patterns, and sex differences within them.

The archaeological evidence for technological and social change through time following the introduction of farming in Central Europe is vast. Despite a paucity of existing biomechanical analyses, this cultural context documents ample potential for long-term impacts on lower limb loading and mobility, in ways that may have differed among men and women. In the Early Neolithic of Central Europe (~7000–5000 BC), the earliest farming communities, the Linear Pottery cultures or *Linearbandkeramik* (LBK), raised a variety of domesticated animals and practiced intensive agriculture, growing primarily cereals (various species of wheat and barley) and garden plants (Milisauskas, 2002) as well as

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exploiting a wide range of wild fish and animals (Müller, 1964). Isotopic analyses of LBK skeletal remains at Vedrovice (Moravia), Schwetzingen (Germany), Stuttgart-Mühlhausen (Germany), Kleinhadersdorf (Austria), and Nitra (Slovakia) provided evidence of migration and patrilocal marriage systems (Price et al., 2003; Richards et al., 2008; Smrčka et al., 2008; Bentley et al., 2012; Zvelebil and Pettitt, 2012) as well as social differentiation that affected access to preferred soils among males (Bentley et al., 2002) and to animal proteins between the sexes (Smrčka et al., 2005; Jarosova, 2008; Richards et al., 2008). No archaeological evidence of wheeled vehicles or early plows have been found from the LBK sites in Central Europe, suggesting that agriculture and travel at this time may have required fairly high lower limb loading. The environment was still largely woodland, providing grazing for livestock but requiring clearance prior to cultivation (Whittle, 1996), with fields then tended manually with digging sticks and crops harvested using flint sickles with wooden handles (Milisauskas, 2002). Most LBK fields were located in thick loess soils in very close proximity to both a settlement and to a river (Lüning, 1982; Kreuz, 1990; Whittle, 1996). The close proximity of cultivated fields and settlements suggests that terrestrial mobility in individuals primarily involved in farming tasks may not necessarily have been particularly high. In addition, water transport likely facilitated the trade and exchange of raw materials and finished objects, due to the difficulty of mobility on foot through still heavily forested land (Milisauskas, 2002).

The introduction of simple ox-drawn plows in the Middle Neolithic (after ~4000 BC) not only allowed for greater crop yields and the expansion of farmland into previously unworkable areas (Milisauskas and Kruk, 2002), but also may have brought significant changes in the relative importance of males and females in food production and the economy (Gimbutas, 1991). Wheeled vehicles first began to appear in Europe in the Middle to Late Neolithic, between approximately 3500–3000 BC (Bakker et al., 1999; Sherratt, 2006), and they were present in Central Europe by at least the Late Neolithic (Banner, 1956; Němejcová-Pavúkova, 1973; Kalicz, 1976). Pack animals and domesticated horses likely also played a crucial role in transportation and in trade (Harding, 2000; Milisauskas and Kruk, 2002). The Middle Neolithic (~5000–3000 BC) is also when metallurgical activities appear, such as the mining of ore and the smelting and casting of copper; these were particularly advanced in the Vinča culture of SE Europe (Milisauskas and Kruk, 2002). These technological innovations of the Middle to Late Neolithic played a major role in driving economic and sociopolitical change (Milisauskas and Kruk, 2002). They may also have substantially altered lower limb loading and/or mobility patterns in one or both sexes, as well as the division of labor by sex.

By the Early Bronze Age (EBA; ~2200–1500 BC), the production of metal objects was an everyday craft activity, requiring newfound technological skill and specialization. A wide variety of objects of economic and social importance were produced at this time, able to be traded and to represent wealth and social ranking (Harding, 2002). Specialized metallurgical activities were likely male-dominated (Milisauskas, 1978) but may have been more likely to produce sex differences in upper limb loading rather than lower limb loading. Metallurgy was accompanied by the expansion of trade and exchange (Duberow et al., 2009); by the Late Bronze Age (~1300–800/750 BC), trading routes connecting the southern and northwestern regions of Europe were well-established (Collis, 1984).

At this time in Austria, intensified trade and exchange has been shown to have primarily affected male craniofacial morphology relative to that of females, though EBA Austrian females still showed evidence of higher migration rates than males due to patrilocal marriage systems (Pellegrini et al., 2011). Existing biomechanical evidence from the postcranium, specifically femoral and tibial diaphyseal morphology, in agriculturalists from Austria, Bohemia and Moravia has not shown any significant diachronic change between the Late Copper Age and the EBA in these regions (Sládek et al., 2006a,b). This may reflect the continued importance of agriculture and the rearing/tending of livestock for EBA food production (Harding, 2002; Bartelheim, 2009), as well as similarity in modes of transportation, including travel by foot, wheeled vehicle or horse, and boats (Harding, 2000, 2002). It appears that, despite more complex socioeconomic organization in the Bronze Age, change in mobility patterns occurred slowly and/or only among a subset of the individuals at a time.

The considerable overlap between bronze and iron goods in the archaeological record of Central Europe (Collis, 1984; Wells, 2002) suggests that bronze and iron production occurred largely simultaneously. Through the Late Bronze Age (~1300–800/750 BC) and Early Iron Age (~800/750–450 BC) transition, bronze was consistently used for the production of common farming/woodworking implements (axes, sickles) and a multitude of weapons and armor (Harding, 2002; Wells, 2002). Subsistence economy also remained fairly consistent into the Early Iron Age, still heavily based in cereals and garden crops (Küster, 1992). Carbonized plant remains from the Serbian (Vojvodina) site of Gomolava in the Carpathian Basin document the remarkably long-term dominance of einkorn wheat (*Triticum monococcum*) across Middle Neolithic (~5000 cal BC) through La Tène (~150 BC) layers in this region (van Zeist, 1975), though other varieties of domesticated wheat, barley, and millet were also important. Seed remains at Gomolava gradually increased in abundance as population density increased and methods of preparation and threshing changed (Bottema and Ottaway, 1982).

Though there are elements of consistency in metallurgical techniques and subsistence through the Bronze and Iron Ages in Central Europe, increasing social and technological complexity did substantially alter the efficiency with which food could be produced and the activities in which members of society specialized. These changes may be expected to have altered habitual behavior patterns and lower limb loading in Central European Iron Age communities, or perhaps altered the way in which activities were allocated within and between the sexes. Iron Age settlements were often much larger and more specialized than those of previous farming communities, frequently forming major and substantially fortified trade centers (Härke, 1979). This greater urbanization and population density may be expected to have played a role in the degree to which high terrestrial mobility would have been a part of everyday life. Task specialization was high in the Iron Age, with important activities including not just metallurgy and agriculture but also woodworking, textile and leather production, mining, gold-smithing, and the production of pottery and glass, amongst others (Wells, 2002). Such a high degree of social complexity likely resulted in inter-individual variation in the degree to which the lower limbs would have been loaded during habitual activities, perhaps restricting high mobility levels to a particular subset of the population.

By the time iron artifacts were pervasive, their complexity indicates the presence of considerable task specialization and the establishment of industrial metal production (Collis, 1984). Because iron ores were widely available across Europe, smiths would have had to rely less on the extensive trade systems set up to move around copper and tin (for bronze) and a variety of other raw materials and objects (Wells, 2002), which may have had implications for mobility patterns. In addition, by the Late Iron Age (~200 BC), technological improvements made possible by iron (such as plowshares and coulters for breaking soil, scythes, shovels, and hoes) had allowed for less desirable land to be exploited, and

more efficiently so (Wells, 2002). Horseback riding is also known to have played a particularly large role in the mobility of Late Iron Age Scythian communities in the Eastern Carpathian Basin, for whom large animal husbandry, particularly of horses, was very important (Bóna, 1987; Rolle, 1989). Social complexity in the Central European Early Medieval period was similarly high as well, and Slavonic groups in Austria show evidence of differential diet and behavior by sex (Schutkowski, 1995; Schutkowski et al., 1999; Herold, 2008).

Though no systematic investigation of the impact of these major socioeconomic and technological changes on Central European lower limb bone cross-sectional morphology has yet been published, long-term trends in European Holocene upper and lower limb bone biomechanics and sexual dimorphism have begun to document the antiquity of sedentary behaviors and declining bone strength and mobility in humans. Preliminary results from published abstracts suggest that, in a large sample of skeletal remains from the European Holocene, lower limb shafts became more circular until about 5000 BP and declined in bending strength until about 2000 BP, with slight increases in the Medieval period (Holt et al., 2012). Other preliminary work also suggests a broad trend of declining sexual dimorphism in femoral anteroposterior robusticity and tibial bending strength from the Neolithic through to modern period in a large European sample (Berner et al., 2012). However, results have not yet been published. The majority of published evidence on lower limb diaphyseal morphology in human populations practicing predominantly farming modes of subsistence documents variable adaptive change (Ruff and Hayes, 1983; Bridges et al., 2000; Sládek et al., 2006a,b; Wescott and Cunningham, 2006; Carlson et al., 2007; Sparacello and Marchi, 2008; Marchi et al., 2011; Sparacello et al., 2011).

There is also considerable evidence in the literature for a decline in sexual dimorphism in femoral and tibial midshaft robusticity from pre-agricultural to agricultural and then industrial/modern societies (e.g., Ruff and Hayes, 1983; Ruff, 1987, 1992, 1994, 1999; Ruff and Larsen, 1990; Marchi, 2008), driven primarily by declining male anteroposterior strengthening of these elements (Ruff, 1987; Ruff et al., 1984; Ruff and Larsen, 1990). However, many studies document no change in sexual dimorphism in lower limb robusticity over time, while others show greater change in females rather than males (Bridges, 1989; Mays, 1999; Bridges et al., 2000; Marchi et al., 2006; Carlson et al., 2007; Sparacello and Marchi, 2008). Among modern foraging populations with high workloads (!Kung, Ache, Igloolik), time allocation and energy expenditure do suggest that physical activity is higher in males than females (Leonard and Robertson, 1992; Katzmarzyk et al., 1994), but the picture is considerably more complex among modern agro-pastoralists. Relative workload between males and females in modern farming populations is much more variable than in foraging populations, with higher physical activity in males in the case of some populations (India, Nepal) and the reverse trend in others (Upper Volta and particularly in the Gambia) (Panter-Brick, 1996). The sexual division of labor in both modern and past agricultural societies is clearly variable and dependent on context and ecology, thus highlighting the importance of controlling for spatial variation in diachronic studies assessing sex differences in behavior through long-term cultural change.

The biomechanical analyses described above all exploit the relationship between mechanical loading and the cross-sectional distribution of bone. Mechanical loading drives plasticity in diaphyseal bone distribution through functional adaptation, a process whereby the structural competence of a bone is maximized to the prevailing loading conditions through the addition of bone where required and its removal where no longer necessary (Garn, 1972; Ruff, 2008; Gosman et al., 2011). Though some caution in the interpretation of *in vivo* loading from bone cross-sectional geometry is warranted (e.g., Jurmain, 1999; Lieberman et al., 2004; Pearson and Lieberman, 2004; Wescott, 2006; Wallace et al., 2014), functional adaptation to loading does appear to alter the cross-sectional distribution of bone in a manner that corresponds to both the intensity and direction of loading (e.g., Ruff et al., 1994; Haapasalo et al., 1996, 2000; Bradney et al., 1998; Stock and Pfeiffer, 2001; Kontulainen et al., 2002; Weiss, 2003; Nikander et al., 2006; Vainionpää et al., 2007; Macdonald et al., 2009; Shaw and Stock, 2009a,b; Warden et al., 2009; Shaw, 2011).

Thus, through the application of an engineering-based beam model to long bone diaphyses, mechanical performance can be quantified by the calculation of cross-sectional geometric (CSG) properties. These provide estimates of compressional strength (total subperiosteal area; *TA*), bending and torsional rigidity (polar second moment of area; *J*), and bone distribution in perpendicular cross-sectional planes (I_{max}/I_{min} and I_x/I_y) (Ruff and Hayes, 1983; Ruff, 2008). Biomechanical analyses using CSG properties have shown strong associations between high levels of terrestrial mobility and particularly high compressional strength (*TA*) and bending and torsional rigidity (*J*), as well as greater anteroposterior (A-P) strengthening (high I_x/I_y) and lower circularity (high I_{max}/I_{min}) of femoral and tibial diaphyses in past human groups (Ruff et al., 1984; Ruff, 1987; Stock and Pfeiffer, 2001, 2004; Holt, 2003; Stock, 2006; Stock et al., 2010).

Utilizing this biomechanical approach, the current study aims to characterize long-term trends in Central European lower limb diaphyseal morphology across ~6150 years following the transition to agriculture in the region. Femoral and tibial CSG properties (*TA*, *J*) and shape indices (I_{max}/I_{min}, I_x/I_y) derived from three-dimensional (3D) laser scans are used to systematically track trends in lower limb loading through time and to identify more specifically the timing of the shift to lower bone robusticity that is typical of broader Holocene European trends. Lower limb loading is expected to be highest in the Neolithic period, due to the relative lack of technological complexity in agricultural implements and transport methods. Given the gradual change in lower limb robusticity identified between the Central European Copper and Bronze Ages by Sládek et al., 2006a,b, temporal trends between the Bronze and Iron Ages in the region are also expected to be gradual. However, high task specialization in the Iron Age has the potential to reduce population-wide signatures of mobility by creating more varied lower limb loading regimes among individuals, and may thus cause declines in overall mean lower limb mechanical variables when these individuals are pooled together. Additionally, given the variability of relative workloads between the sexes in modern agro-pastoralist communities, it is unclear to what extent there will be sexual dimorphism in lower limb morphology in the current study. Existing evidence of dietary and health differentiation by sex in skeletal remains from Central Europe suggest that some degree of sex-specificity to temporal trends in lower limb bone morphology may be expected.

1. Materials and methods

1.1. Skeletal sample

The skeletal series that were analyzed are from archaeological populations with similar subsistence strategies (primary reliance on domesticated crops and livestock; Milisauskas, 2002) and originally excavated from southern Germany, Lower Austria, western Slovakia, Hungary, Czech Republic (Moravia), and northern Serbia (Vojvodina) (Fig. 1). Skeletal remains were obtained from museum and university collections (see Table 1) and represent portions of four time periods following the transition to agriculture: the Early and Middle Neolithic (~5300–4600 cal BC), Early and Middle

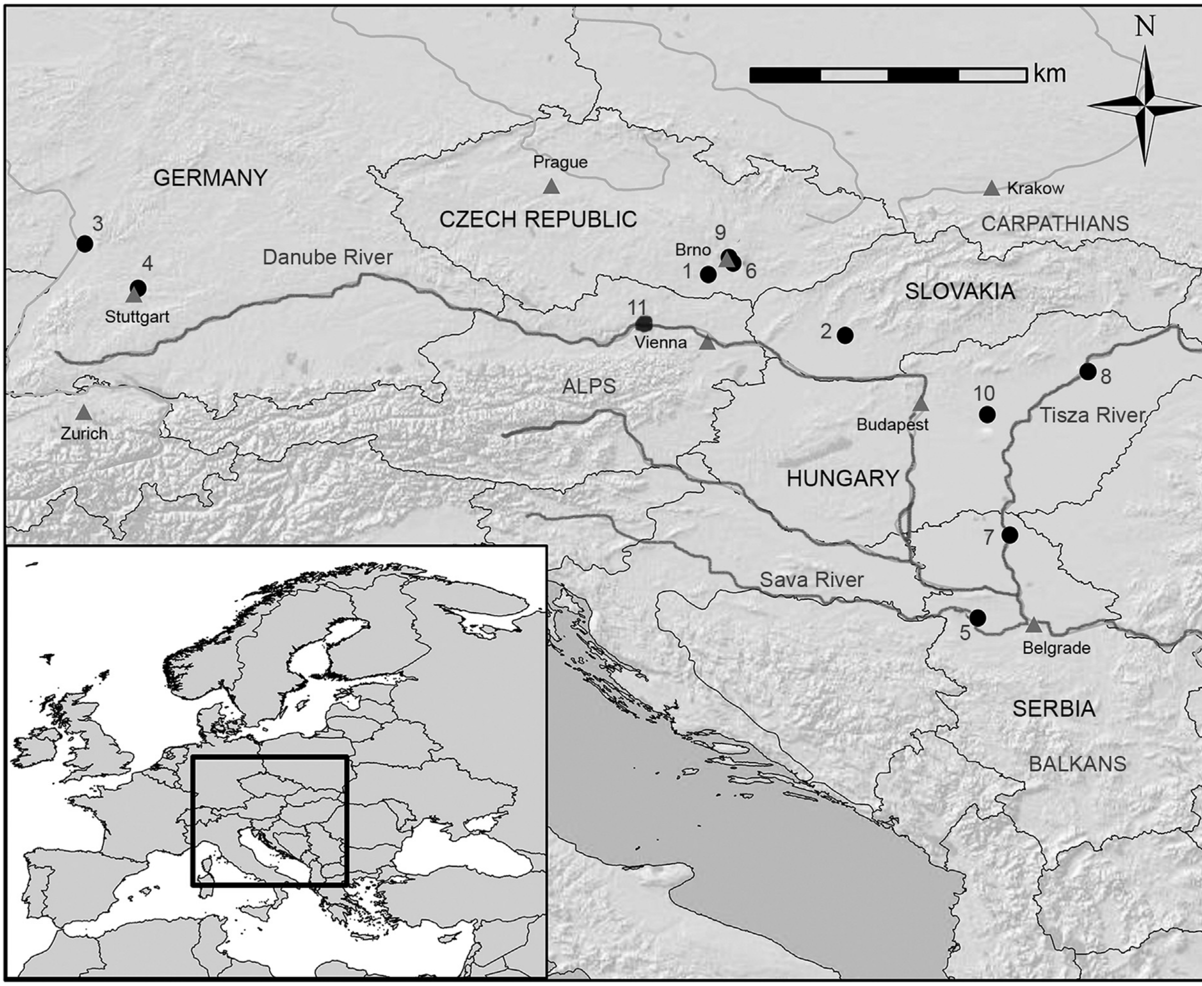

Fig. 1. Map of Central Europe indicating the sampled cemeteries in approximate chronological order: 1. Vedrovice 2. Nitra Horné Krškany 3. Schwetzingen 4. Stuttgart-Mühlhausen 5. Hrtkovci-Gomolava 6. Brno-Tuřany 7. Ostojićevo 8. Polgár Kenderföld 9. Brno-Maloměřice 10. Tápiószele 11. Pottenbrunn.

Bronze Age (~2200–1450 BC), Early through Late Iron Age (~850BC–100 AD), and Early Medieval (~800–850 AD) periods. Where possible, skeletal series from multiple time periods within the same local region were obtained in an attempt to reduce influences other than behavior and mobility on lower limb robusticity. These may include climate/latitude (Pearson, 2000; Stock, 2004, 2006) and uneven and/or steep terrain (Ruff, 1987, 1995, 1999, 2005b; Stock and Pfeiffer, 2001; Marchi, 2008; Sparacello and Marchi, 2008).

Aging and sexing was performed by AAM and Abigail Ash (University College Dublin), according to the methods outlined in Buikstra and Ubelaker (1994). Only skeletally mature adults were included in analyses and, when possible to age more specifically than "adult", preference was given to the inclusion of adults under the age of approximately 40 years. This was done in order to reduce the effects of age-related differences in cortical thickness among individuals on mechanical property estimates; beginning at the age of ~40 years, endosteal resorption begins, resulting in the expansion of the medullary cavity (Trinkaus et al., 1994) and relatively greater responsiveness of the endosteal bone to mechanical loading (Ruff et al., 1994). These endosteal changes in older adults cannot be accounted for with surface scanning methods of quantifying CSG properties, but sample size and preservation considerations meant that some age variation within and between samples was unavoidable. Also, it was not possible to age some individuals more specifically than "skeletally mature adult", so the exploration of age differences was not possible in the current study. However, the numbers of adults aged definitively as greater than 40 years at death was small (16 of 228 femora and 23 of 215 tibiae) and are not expected to have drastically affected temporal trends. Thus, this small number of individuals aged older than 40 years at death were included in analyses in order to maximize sample sizes.

1.2. Laser scanning procedure

Due to typically low levels of asymmetry in lower limb bone diaphyses, only the best-preserved femur and tibia of each individual was laser scanned (Auerbach and Ruff, 2006). Preference was given to the right side if both elements were equally well preserved. A portable NextEngine desktop laser scanner was used to obtain three-dimensional (3D) images of entire bones. Three-dimensional models were composed of 10 individual scan surfaces taken in a 360° rotation around the bone, as well as individual scans of proximal and distal joint surfaces. Scans were taken using at least the minimum HD quality setting available in the ScanStudio HD Pro (version 1.3.2) (quoted as 2.2k ppi). Laser scan images were trimmed, aligned and fused using ScanStudio HD Pro and Rapidform XOR. All bones were oriented through the realignment of *x*-, *y*- and *z*-axes to anatomical planes following definitions found in Ruff (2002). Further details of the laser scanning procedure applied have been reported previously (Davies et al., 2012).

Table 1
Central European population details.

Time period and culture	Approximate Date (BC)[a]	Cemetery	Cemetery location	Collection housed at:	Individuals (males/females)
Neolithic					**95 (55/40)**
Early					
LBK	5300–5100[a]	Vedrovice	Czech Republic	Moravian Museum (Brno)	21 (10/11)
LBK	5370–4980[a]	Nitra Horné Krškany	Slovakia	Moravian Museum (Brno)	16 (8/8)
LBK	5260–5010[a]	Schwetzingen	Germany	Stuttgart Regional Council, State Conservation Office-Osteology (Konstanz)	21 (11/10)
LBK	5200–4960[a]	Stuttgart-Mühlhausen	Germany	University of Tübingen	28 (17/11)
Middle					
Vinča	~4950–4600[a]	Hrtkovci-Gomolava	Serbia	Museum of Vojvodina (Novi Sad)	9 (9/0)
Bronze Age					**74 (39/35)**
Early					
Únětice	2200–2000	Brno-Tuřany	Czech Republic	Masaryk University (Brno)	15 (9/6)
Maros	~1600/1500	Ostojićevo	Serbia	National Museum of Kikinda	44 (21/23)
Middle					
Füzesabony	1550–1450	Polgár Kenderföld	Hungary	Hungarian Natural History Museum (Budapest)	15 (9/6)
Iron Age					**57 (27/30)**
Early					
Bosut	850–600/500	Hrtkovci-Gomolava	Serbia	Museum of Vojvodina (Novi Sad)	21 (9/12)
Middle					
Celtic	400–200	Brno-Maloměřice	Czech Republic	Moravian Museum (Brno)	16 (11/5)
Late					
Scythian	385–100 AD[a]	Tápiószele	Hungary	Hungarian Natural History Museum (Budapest)	20 (7/13)
Early Medieval					**22 (11/11)**
Slavonic	~800–850 AD	Pottenbrunn	Lower Austria	Vienna Natural History Museum	22 (11/11)

[a] Indicates calibrated radiocarbon date; LBK = *Linearbandkeramik*; approximate dates from: Friesinger, 1972; Tasić, 1972; Ubelaker and Pap, 1998; Tasić 2003–2004; Pettitt and Hedges, 2008; Borić, 2009; Bentley et al., 2012; Fischl et al., 2013; Whittle et al., 2013; Eva Drozdová, pers. comm., Zdeněk Tvrdý, pers. comm.

1.3. Quantification of midshaft CSG properties and shape indices

Because laser surface scans do not provide information on endosteal contours, CSG properties were derived from periosteal information only. However, because bone fibers furthest from the neutral bending axis or centroid during bending and/or torsion (twisting) resist the majority of stresses (Jepsen, 2009), the redistribution of bone periosteally maximizes structural integrity (Ruff, 2008) and thus periosteal bone is particularly biomechanically important. Though imaging of both periosteal and endosteal contours is ideal for the calculation of CSG properties, the mechanical relevance of periosteal bone in particular has allowed for very accurate estimates of true CSG properties to be derived from external contours alone at midshaft (Stock and Shaw, 2007; Sparacello and Pearson, 2010) and across large portions of mid-femoral and mid-tibial diaphyses (Macintosh et al., 2013).

Cross-sectional properties were calculated from finished models for every 5% of maximum bone length (taken parallel to the long axis of the diaphysis) using custom-built AsciiSection software (Davies et al., 2012). This software uses equations for polygons to calculate CSG properties and shape indices for the periosteal contour at individual diaphyseal cross sections. For the purposes of this study, the midshaft (50% of maximum bone length) section location was analyzed, as midshaft CSG in the femur and tibia has shown a high correspondence with terrestrial mobility (Stock, 2006). The CSG properties used in this study were the total subperiosteal area of the section (*TA*), an estimate of compressional strength, the polar second moment of area (*J*), which reflects twice average bending and torsional rigidity, and bone cross-sectional shape ratios about the major and minor axes (I_{max}/I_{min}) and A-P (*x*) and M-L (*y*) axes (I_x/I_y) (Ruff and Hayes, 1983; Ruff, 2008). All CSG properties utilized in this research are presented in Table 2.

1.4. Size-standardization and analytical methods

The effect of body size differences on lower limb cross-sectional geometry was controlled for by standardizing both *TA* and *J* to appropriate measures of body size, following the method of Ruff (2008): *TA*/estimated body mass, *J*/((estimated body mass * (maximum bone length^2)). Maximum bone lengths parallel to the long axis of the diaphysis were recorded using an osteometric board, and body mass was estimated utilizing the equations for European Holocene populations derived by Ruff et al. (2012), from an average of measurements from the left and right lower limbs. All outliers greater than three standard deviations from the mean were removed from the data prior to analyses. Cross-sectional geometric properties were compared through time by sex using one-way analysis of variance (ANOVA) and Hochberg's GT2 or Games-Howell post-hoc tests. Independent samples *t*-tests were used to examine sexual dimorphism within each time period.

Table 2
Description of CSG properties and shape indices used.

Variable	Formula	Biomechanical or morphological relevance
Total subperiosteal area (*TA*)	–	Highly correlated with cortical area, a measure of compressional strength
Polar second moment of area (*J*)	$I_{max} + I_{min}$	Torsional and twice average bending rigidity in any two perpendicular planes
Shape ratio	I_{max}/I_{min}	Distribution of bone about the major and minor axes of a cross-section
Shape ratio	I_x/I_y	Distribution of bone about the A-P and M-L axes of a cross-section

TA = mm^2; J = mm^4; I_{max}, I_{min} = second moments of area about maximum and minimum axes (maximum and minimum bending rigidity; mm^4); I_x, I_y = second moments of area about anteroposterior (A-P) and mediolateral (M-L) axes (A-P and M-L bending rigidity; mm^4); descriptions from Ruff and Hayes (1983), Ruff (2008).

Pearson's correlations were used to test the correspondence between proximal femoral cross-sectional properties and body size-related variables. Statistical analyses were conducted in SPSS v20.

2. Results

Summary statistics for midshaft CSG properties by bone and time period are presented in Table 3. Midshaft CSG properties by sex and time period are plotted for the femur and tibia in Figs. 2 and 3, respectively. All results of one-way ANOVAs by bone and sex are summarized in Table 4. Among males, significant temporal change is found almost exclusively in the tibia, documenting progressive gracilization through time. Both tibial midshaft *TA* (Fig. 3A) and *J* (Fig. 3B) are significantly higher in Neolithic males than Iron Age and Medieval males, and tibial midshaft I_{max}/I_{min} (Fig. 3C) is significantly higher in Neolithic males than Medieval males. The temporal gracilization documented in male tibiae is paralleled in femoral midshaft I_x/I_y (Fig. 2D): Neolithic males have significantly higher ratios (greater anteroposterior strengthening) than Iron Age and Medieval males. Significant temporal change is less pronounced among females, though midshaft tibial shape ratios follow a similar trend to that seen among males: Neolithic females have significantly higher I_x/I_y than Iron Age females (Fig. 3D) and significantly higher I_{max}/I_{min} than Iron Age and Medieval females (Fig. 3C). Among female femora, midshaft *TA* and *J* rise significantly from the Bronze Age into the Iron Age (Fig. 2A and B); Iron Age females have very high mean femoral *TA* and *J* relative both to contemporaneous males and to all other females.

Results of independent samples *t*-tests for sex differences in CSG properties and shape indices by time period and bone are provided in Table 5. Where significant, sexual dimorphism almost always reflects higher values in males than in females. In the Neolithic period, sexual dimorphism is pronounced: males have significantly higher femoral shape ratios and tibial *TA* and *J* than females, as well as tibial I_{max}/I_{min}. High sexual dimorphism extends into the Bronze Age: males have significantly higher femoral and tibial *TA* and *J* than females, as well as higher femoral I_x/I_y and tibial I_{max}/I_{min}. Sexual dimorphism in the Iron Age and Medieval periods is much reduced and is found almost exclusively in the shape ratios. Iron Age males have significantly higher tibial I_{max}/I_{min} (less circular) and femoral and tibial I_x/I_y (more elongated in the A-P plane) than females. In the Medieval period, males have significantly higher femoral I_{max}/I_{min} (less circular) and *J* (higher bending and torsional rigidity) than females, but female tibiae have higher I_x/I_y (greater elongation in the A-P plane) than males.

The strongest temporal trends in both sexes are found in the tibia, in midshaft *J* among males and midshaft I_{max}/I_{min} among females. These strong temporal trends are examined by cemetery in order to determine whether or not they are reflecting an average of a more complex regionally variable pattern through time. Summary statistics by cemetery (in approximate chronological order) in male tibial midshaft *J* and female I_{max}/I_{min} are presented in Table 6. Among males, the high tibial bending and torsional rigidity (*J*) typical of Neolithic male tibiae is present right through to the Middle Bronze Age (with the exception of Vojvodina cemeteries; see below) (Fig. 4A), after which a shift to lower tibial *J* occurs, resulting in lower values from the Early Iron Age through to the Early Medieval period. Early Neolithic LBK males at Schwetzingen exhibit significantly higher tibial *J* than Early Iron Age (Brno-Maloměřice, Tápiószele) and Early Medieval (Pottenbrunn) males, while LBK males from Stuttgart-Mühlhauen and Vedrovice (Moravia, Czech Republic) also exhibit significantly greater tibial *J* than Early Medieval males from nearby Lower Austria. In addition, regional variation in male tibial rigidity is identified: tibial *J* in males from the Vojvodina region of northern Serbia (Gomolava and Ostojićevo, identified by an asterisk in Fig. 4A) stands out from contemporaneous males as being particularly low, to an extent not reached by all Central European males until the Early Iron Age. Males from the Vojvodina region of Serbia have significantly lower tibial *J* than Early Neolithic German LBK males at Stuttgart-Mühlhausen (vs. Ostojićevo) and Schwetzingen (vs. both Gomolava and Ostojićevo). For comparison, the pattern of temporal change and regional variation identified in male tibial *J* is not reproduced in female tibial *J* by cemetery.

Table 3
Midshaft summary statistics by bone and time period.

Population	N	Males				N	Females			
		TA		*J*			*TA*		*J*	
		Mean	SD	Mean	SD		Mean	SD	Mean	SD
Femur										
Neolithic	50	8.583	0.914	38.320	6.586	38	8.317	0.686	36.239	5.893
Bronze Age	37	8.454	1.048	38.343	7.694	30	7.865	0.812	33.328	6.464
Iron Age	20	8.409	0.908	38.402	7.273	29	8.534	0.976	39.404	8.046
Medieval	11	8.655	0.874	42.820	6.685	9	8.194	1.002	33.140	5.796
Tibia										
Neolithic	50	7.426	0.830	47.854	9.597	31	6.352	0.779	35.014	7.268
Bronze Age	32	6.980	0.942	42.780	9.217	29	6.174	0.816	31.752	6.498
Iron Age	19	6.731	0.622	38.153	6.098	17	6.354	0.812	33.982	8.091
Medieval	10	6.463	0.578	36.698	5.311	11	6.335	0.878	31.618	7.360
	N	I_{max}/I_{min}		I_x/I_y		*N*	I_{max}/I_{min}		I_x/I_y	
		Mean	SD	Mean	SD		Mean	SD	Mean	SD
Femur										
Neolithic	50	1.323	0.164	1.180	0.224	39	1.250	0.142	0.973	0.159
Bronze Age	37	1.261	0.117	1.062	0.170	31	1.271	0.191	0.909	0.179
Iron Age	20	1.264	0.174	1.009	0.222	29	1.263	0.205	0.889	0.151
Medieval	11	1.289	0.108	0.991	0.213	11	1.185	0.065	0.993	0.170
Tibia										
Neolithic	50	2.458	0.398	1.710	0.308	34	2.243	0.412	1.805	0.396
Bronze Age	35	2.354	0.402	1.655	0.294	32	2.116	0.319	1.596	0.361
Iron Age	23	2.214	0.365	1.678	0.324	20	2.010	0.231	1.481	0.206
Medieval	10	2.049	0.457	1.479	0.166	11	1.865	0.240	1.685	0.232

N: number of bones included in analyses; SD: standard deviation.

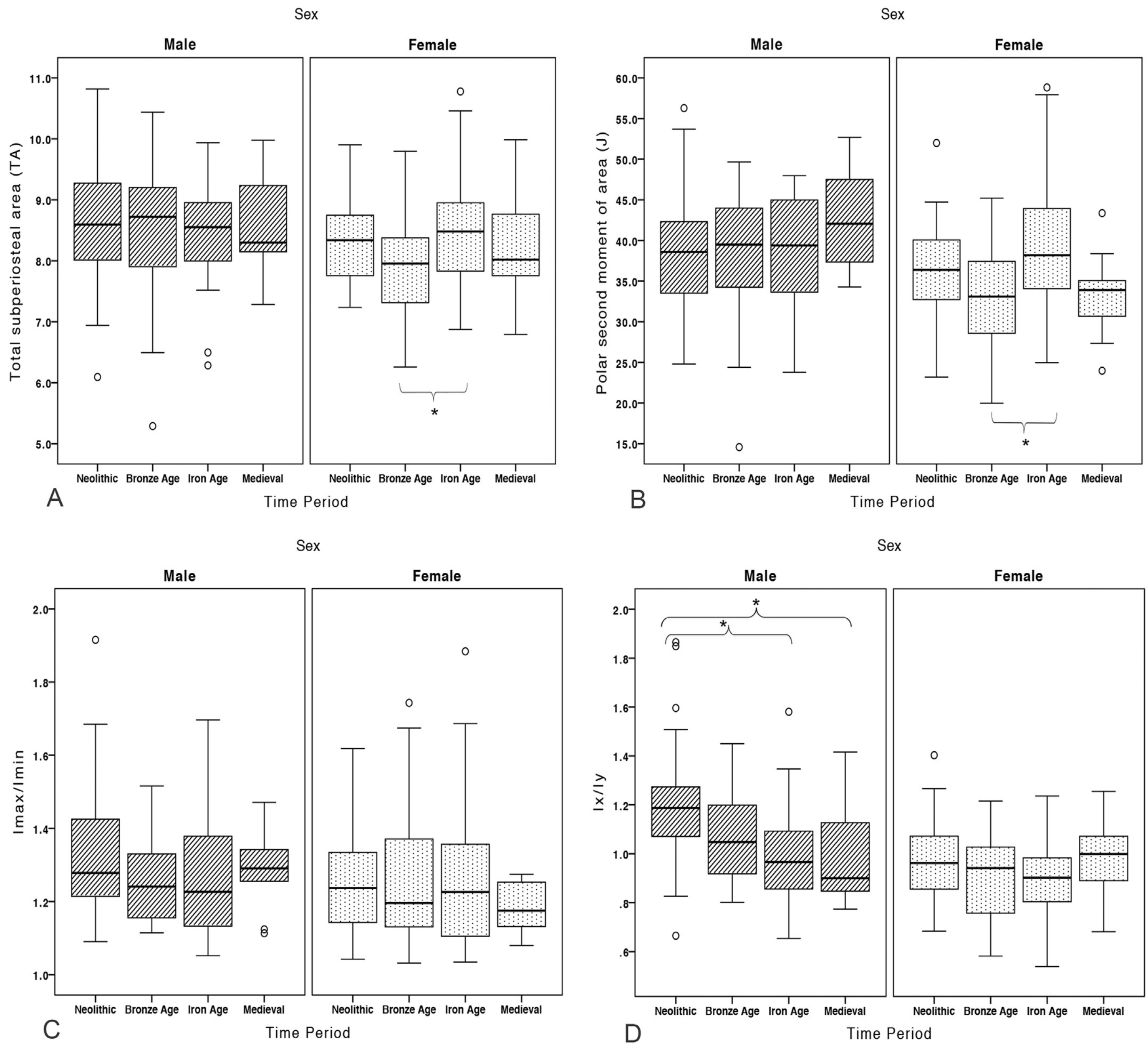

Fig. 2. Femoral midshaft boxplots by sex and time period for A) total subperiosteal area: *TA*, B) polar second moment of area: *J*, C) I_{max}/I_{min}, and D) I_x/I_y. Brackets denote change significant at either $p < 0.05$ (*) or $p < 0.001$ (**).

Among females, strong declines in midshaft tibial I_{max}/I_{min} by time period are tracking a gradual increase in circularity through time that is remarkably consistent across all twelve cemeteries in the Central European region (Fig. 4B). Early Neolithic LBK females from the oldest cemetery included in analyses, Vedrovice (Moravia, Czech Republic), have significantly higher I_{max}/I_{min} (less circular tibial cross-sections) than females from the most recent cemetery, Early Medieval Pottenbrunn (Lower Austria). For comparison, among males, midshaft tibial I_{max}/I_{min} by cemetery exhibits a similar gradual trend through time with no regional variation (in contrast to the pattern seen in tibial *J*), but this trend is not significant.

3. Discussion

This study provides some of the first reported evidence of systematic long-term change in lower limb cross-sectional geometry among preindustrial Central Europeans in the ~6150 years following the transition to agriculture in the region. It also documents sex-specific variation in the response to long-term cultural change at this time. Though trends were indicative of declining mobility in both sexes, these were stronger in males, in whom pronounced changed in tibial bending and torsional rigidity documented a major shift in loading patterns in the Late Bronze Age that was not seen in females. Though trends among females were less pronounced than among males, significant changes were most often temporally progressive, documenting a gradual decline in mobility that was consistent across Central Europe.

Cross-sectional dimensions, particularly of the tibia, were indicative of high terrestrial mobility in Early Neolithic LBK males and females relative to later groups. One possibility for why LBK lower limb loading may have been so high is suggested by strontium isotope analyses of LBK individuals at Schwetzingen, Stuttgart-Mühlhausen, Nitra, and Vedrovice. These analyses document a

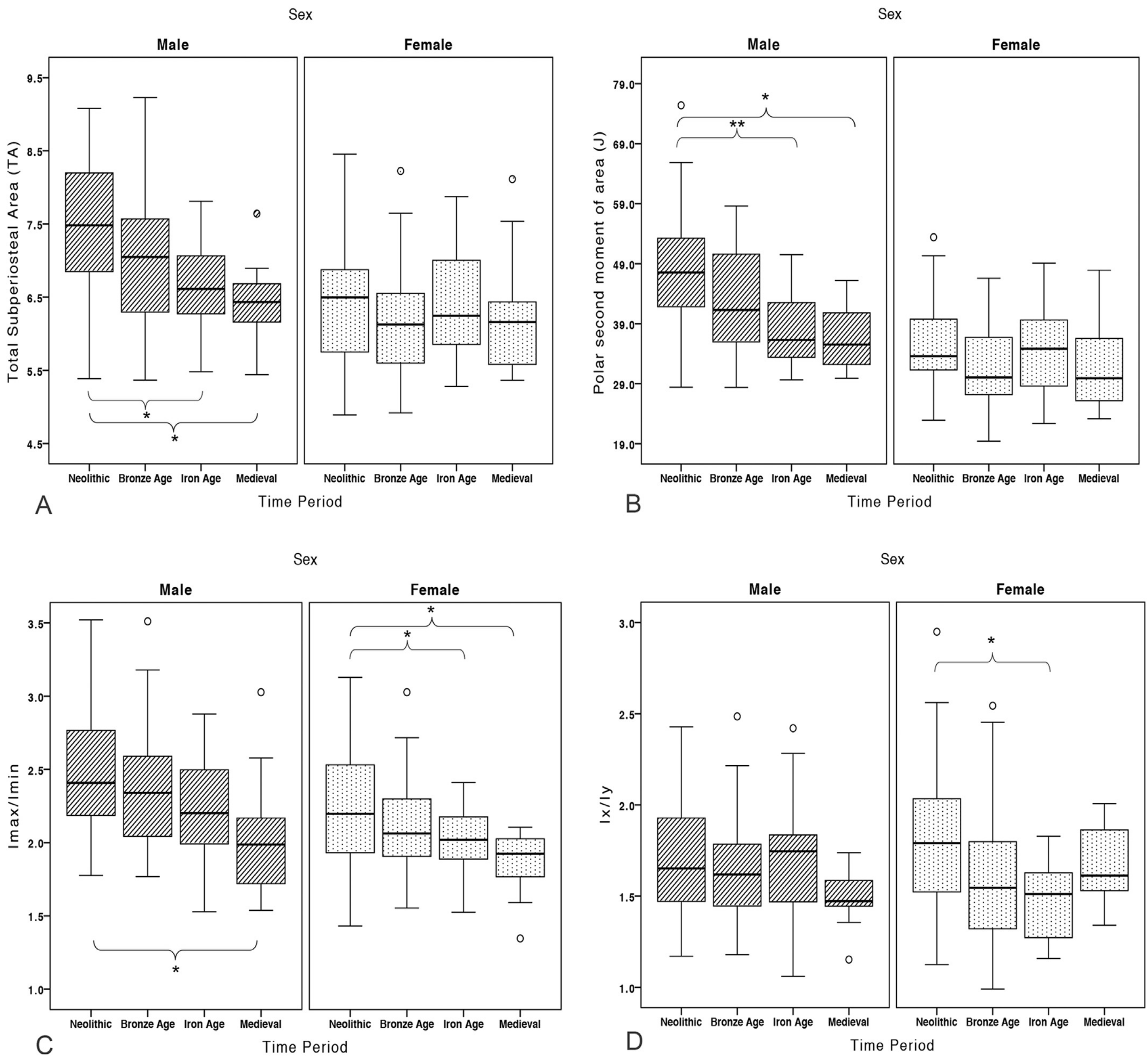

Fig. 3. Tibial midshaft boxplots by sex and time period for A) total subperiosteal area: *TA*, B) polar second moment of area: *J*, C) I_{max}/I_{min}, and D) I_x/I_y. Brackets denote change significant at either $p < 0.05$ (*) or $p < 0.001$ (**).

Table 4
Results of one-way ANOVAs by bone and sex.

	Bone		Significance				
			Neo vs.			BA vs.	
	Femur	Tibia	BA	IA	Med	IA	Med
Male							
TA	ns	<0.001	ns	<0.012	<0.006	ns	ns
J	ns	<0.001	ns	<0.001	<0.002	ns	ns
I_{max}/I_{min}	ns	<0.010	ns	ns	<0.022	ns	ns
I_x/I_y	<0.003	ns	ns	<0.016	<0.048	ns	ns
Female							
TA	<0.023	ns	ns	ns	ns	<0.016	ns
J	<0.013	ns	ns	ns	ns	<0.007	ns
I_{max}/I_{min}	ns	<0.006	ns	<0.048	<0.004	ns	ns
I_x/I_y	ns	<0.006	ns	<0.006	ns	ns	ns

All values indicate significant *p*-values below 0.05; ns = not significant at $p < 0.05$; Neo: Neolithic; BA: Bronze Age; IA: Iron Age; Med: Medieval period.

small percentage of non-local individuals interred at the Early Neolithic LBK farming communities included in analyses, and these individuals subsisted at least part of the year on upland resources and were buried in socially distinct ways (Bentley et al., 2002; Price

Table 5
Results of independent samples *t*-tests for sex differences in CSG properties and shape indices by time period and bone.

	Femur				Tibia			
	Neo	BA	IA	Med	Neo	BA	IA	Med
TA	ns	<0.014	ns	ns	<0.001	<0.001	ns	ns
J	ns	<0.006	ns	<0.044	<0.001	<0.001	ns	ns
I_{max}/I_{min}	<0.031	ns	ns	<0.018	<0.019	<0.010	<0.035	ns
I_x/I_y	<0.001	<0.001	<0.029	ns	ns	ns	<0.024	<0.039

All values indicate significant *p*-values below 0.05; ns = not significant at $p < 0.05$; Neo: Neolithic; BA: Bronze Age; IA: Iron Age; Med: Medieval period; all significant results reflect higher values in males with the exception of Medieval tibial I_x/I_y.

Table 6
Summary statistics by cemetery in the midshaft tibial variables exhibiting the strongest temporal change by time period in each sex.

	N	Male J		N	Female I_{max}/I_{min}	
		Mean	SD		Mean	SD
Neolithic						
1. Vedrovice	9	**49.859**	10.543	10	**2.394**	0.405
2. Nitra Horné Krškany	7	45.639	5.691	8	2.302	0.457
3. Schwetzingen	10	**52.609**	8.866	5	2.112	0.457
4. Stuttgart-Mühlhausen	14	**49.645**	9.309	11	2.122	0.363
5. Hrtkovci-Gomolava	9	39.510	8.181	–	–	–
Bronze Age						
6. Brno-Tuřany	8	47.397	6.824	4	2.081	0.167
7. Ostojićevo	19	38.824	8.260	20	2.160	0.344
8. Polgár Kenderföld	5	50.427	8.936	6	1.939	0.279
Iron Age						
9. Hrtkovci-Gomolava	4	39.086	7.956	9	2.039	0.172
10. Brno-Maloměřice	9	38.077	6.347	5	1.946	0.338
11. Tápiószele	6	37.644	5.513	6	2.019	0.239
Medieval						
12. Pottenbrunn	10	36.698	5.311	11	1.865	0.240

N: number of bones included in analyses; SD: standard deviation; bold indicates significance of at least $p < 0.05$ relative to later groups.

et al., 2003; Smrčka et al., 2005). Thus, at the very earliest stages of the transition to farming, individuals obtaining subsistence from hunting/gathering or mixed methods may have joined farming communities; these individuals may have retained signatures of higher mobility over steeper upland terrain than those individuals growing up in a predominantly farming subsistence in the lowland regions of Central Europe. This may explain some of the particularly high CSG properties found at Schwetzingen, Stuttgart-Mühlhausen and Vedrovice. However, the majority of individuals sampled at these sites exhibited isotopic signatures indicative of local origins (Smrčka et al., 2005, 2008; Richards et al., 2008; Zvelebil and Pettitt, 2012). Within the LBK community of Schwetzingen, strontium isotope analyses suggest that males buried without adzes spent much of the year outside of prime loess soil areas (Bentley et al., 2012). These males were likely not heavily involved in agricultural or land clearance activities, and may thus have been primarily responsible for the grazing of domesticated livestock in the surrounding woodlands, perhaps requiring habitually higher lower limb loading and mobility.

The presence of non-local materials in Early Neolithic LBK sites does indicate that long-distance trade and exchange systems were already in place at this time (Milisauskas, 2002), however the still very wooded landscape and lack of major roads/paths would have hampered long-distance travel by foot. Interestingly, the consistent proximity of LBK settlements to rivers (typically within 500 m; Lüning, 1982) suggests that water transport likely played a large part in the long-distance travel and distribution of goods through the Central European region (Harding, 2000, 2002; Milisauskas, 2002). Even with the introduction of simple plows (~4000 BC; Milisauskas and Kruk, 2002) and wheeled vehicles (~3500 BC; Banner, 1956; Kalicz, 1976; Bakker et al., 1999) in the Middle to Late

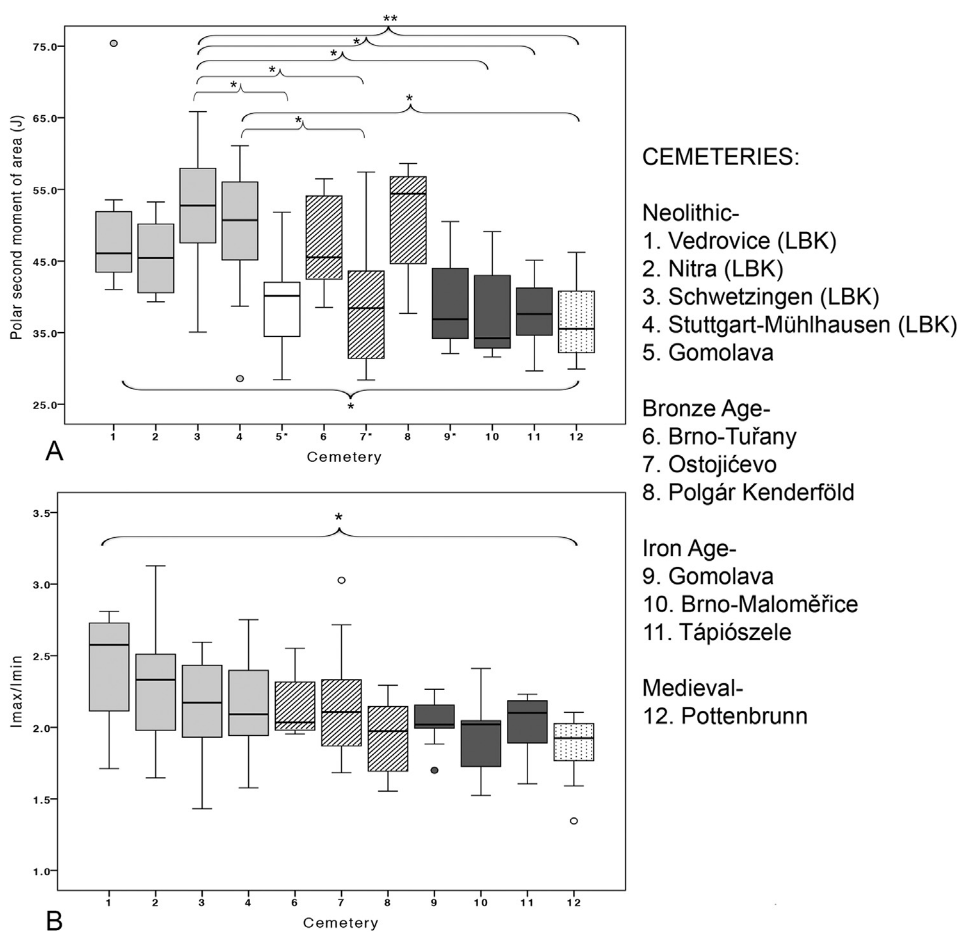

Fig. 4. Tibial midshaft boxplots by cemetery for A) male polar second moment of area (J) and B) female I_{max}/I_{min}. Brackets denote change significant at either $p < 0.05$ (*) or $p < 0.001$ (**). Cemeteries accompanied by an asterisk indicate those from Vojvodina (Serbia).

Neolithic in Central Europe, results provide no indication of any corresponding widespread change in lower limb bone strength among either males or females in the Early Bronze Age.

The lack of significant temporal change in lower limb CSG properties between the Neolithic and Bronze Age groups in either sex is somewhat surprising considering these major technological changes of the Middle to Late Neolithic. It appears that overall temporal changes in lower limb bone morphology from the Neolithic to Bronze Age in Central Europe (with cemeteries pooled) were relatively gradual in both sexes, or were occurring only among a subset of the individuals at a time. Sládek et al.(2006a,b) also found little change in mobility at the late Copper Age (Eneolithic) to Early Bronze Age transition in Central Europe, and this appears to be true when pre-metal Neolithic groups are included as well.

However, Sládek and colleagues suggest that change was mosaic in populations of this region as it underwent complex socioeconomic change. Analyses examining variation between cemeteries in the current study support this view, at least among male tibial CSG properties.

Regional variation in mean male tibial bending and torsional rigidity (*J*) was identified among the Neolithic and Bronze Age groups, with males from the Vojvodina region of northern Serbia demonstrating consistently low values at all time periods investigated, from the Middle Neolithic through Early Iron Age. In contrast, tibial *J* was relatively high and homogeneous among the Early Neolithic LBK males, and these high mean values were maintained into the Middle Bronze Age, at least in Hungary and the Czech Republic. It is possible that the introduction of simple plows and wheeled vehicles in the Middle to Late Neolithic did not occur simultaneously across Central Europe, and perhaps regional variation among Middle Neolithic through Middle Bronze Age males is reflecting this. However, it is only males from the Vojvodina region of Serbia who stand out, producing regional variation within the Great Hungarian Plain itself in the Middle Bronze Age. Contemporaneous males at Polgár Kenderföld (Füzesabony) in the north and Ostojićevo (Maros) in the south of the region display substantially different levels of lower limb loading. It is unclear why this should be the case, though Vojvodina formed a major contact zone that saw the mixing of multiple cultures, being subject to the influences from the northern Carpathian Basin (Pannonian Plain) and the surrounding Carpathians, Balkans, and sub-Alpine regions (Tasić, 2003–2004). Mean values of tibial *J* among males did not converge across Central Europe until the Early Iron Age, at which point mean male tibial bending and torsional rigidity remained low through to the Early Medieval period. The pattern of temporal change in tibial shape ratios among females was much different: strong female declines in tibial cross-sectional circularity (I_{max}/I_{min}) by time period reflected similar unidirectional and gradual declines by cemetery with no evidence of regional variation or punctuated drops with the introduction of new technologies. Rather, female tibiae across Central Europe became progressively and very gradually more circular in cross-section through time following the introduction of agriculture.

Though the social and technological changes of the Middle to Late Neolithic (e.g., plow, wheeled vehicles, early metallurgy) did not appear to cause marked or rapid impacts on lower limb bone morphology in either sex, they did produce major changes in sexual dimorphism and the sexual division of labor. It was in the Bronze Age group (Early to Middle Bronze Age) in which sexual dimorphism was most pronounced and pervasive. Males had significantly higher compressional strength and bending and torsional rigidity in both femora and tibiae than females, as well as more A-P strengthened femora and less circular tibiae.

This high dimorphism is likely due more to progressive declines in female lower limb bone properties, as male lower limb loading, at least in the tibia, remained high in most Early and Middle Bronze Age males (see Table 6). There were no significant differences between the Neolithic and Bronze Age groups, and male tibial *J* was high at both Brno-Tuřany (EBA) and Polgár Kenderföld (Middle Bronze Age). Agriculture in the Bronze Age likely still involved a high degree of lower limb loading to work the plows, and the tilling of land and tending of domesticated livestock remained of primary importance at this time (Harding, 2002). In addition, transportation in the Bronze Age remained largely by foot or by watercraft (Harding, 2002). However, the introduction of simple ox-drawn plows in the Middle Neolithic (~4000 BC) may have reduced the importance of females with digging sticks in agricultural activities, reducing the relative importance of women as food producers and supporting a more patriarchal society (Gimbutas, 1991; Milisauskas and Kruk, 2002). Metallurgical activities involving copper, bronze, and gold were also likely male-dominated (Milisauskas, 1978), while women were probably involved in other craft activities in the Mid/Late Neolithic and EBA, including particularly pottery but also textile production from wool and flax (Milisauskas and Kruk, 2002). Shifting female behaviors in the Bronze Age, and changes in the degree or type of female involvement of in food production, may have resulted in a divergence in lower limb loading between the sexes.

The high male bone strength and sexual dimorphism that was characteristic from the Early Neolithic through Middle Bronze Age in most of Central Europe was in sharp contrast to the widespread and consistently reduced levels of tibial loading levels and sexual dimorphism that distinguished the more recent groups included in the current study: the Early through Late Iron Age and the Early Medieval period. Sexual dimorphism in femoral and tibial CSG properties in the Iron Age and Medieval groups was much reduced relative to the Neolithic and Bronze Age, and mean values of all CSG properties were low in both sexes. Among males, the Early Iron Age marked the beginning of very low mean tibial bending and torsional rigidity that remained as such through at least the Early Medieval period.

Declines in lower limb loading in both sexes are likely reflecting changes in mobility levels attributable to some of the major improvements in technology in the Iron Age and Medieval periods, as well as to the enhanced craft specialization that accompanied them. Plowing and harvesting became much more efficient with the advent of iron plows and colters, scythes, shovels, and hoes (Wells, 2002), enhancing food production and requiring less intensive labor. Iron Age and Medieval trade was extensive and complex, yet results are suggestive of overall low mobility levels, so high trade and exchange was not necessarily associated with high levels of terrestrial mobility. This may be due to the increased importance and use of watercraft, wheeled vehicles and/or horses or to the presence of a specialized merchant class, requiring little terrestrial mobility of the majority of individuals in society.

Though results document diachronic change in lower limb bone morphology in both sexes following the transition to agriculture in Central Europe, particularly strong in males, the characteristics of the loading that were driving these changes remain largely unknown.

In order to better reconstruct the mobility characteristics of Central European males, mean tibial mechanical properties of all males by time period were compared to published means of modern and recent males with known mobility patterns. In Fig. 5, 95% confidence intervals for mean male tibial *J* (Fig. 5A) and I_{max}/I_{min} (Fig. 5B) are plotted with the published means of Andaman Islanders (AI: high marine mobility) from Stock and Pfeiffer (2001), and modern male cross-country runners (CCR: high frequency loading of lower intensity in predominantly one direction), field hockey players (FHP: lower repetitiveness but higher intensity

loading in multiple directions), and sedentary controls (SC: healthy modern non-athletes) from Shaw and Stock (2009b).

The Neolithic male group utilized in the current study had mean tibial bending and torsional rigidity (J) in the range of modern male cross-country runners. This was particularly true of Early Neolithic LBK males at Vedrovice (Czech Republic), Schwetzingen (Germany), and Stuttgart-Mühlhausen (Germany) (Table 6). However, mean tibial I_{max}/I_{min} (index of cross-sectional circularity) in all Central Europeans studied was consistently below that of cross-country runners (Fig. 5B). This suggests that, though Neolithic tibiae were strengthened to a similar degree of bending and torsional loading as modern cross-country runners, this loading may have been less predominantly front-to-back (A-P) than that experienced during long-distance running. It is likely that all Central European males were performing a greater variety of behaviors in their daily lives than the predominantly long-distance forward locomotion of competitive cross-country runners, and this is being reflected by tibiae less predominantly strengthened to loading in one particular direction. While loading intensity among Neolithic males was likely fairly similar to that experienced by modern long-distance runners, the directionality of this loading (tibial I_{max}/I_{min}) was more similar to mean values in Andaman Islander males. It is possible that mobility patterns among Neolithic males could have been similarly mixed, likely with both terrestrial and riverine components. The temporal decline in male mobility in Central Europe is evident from Fig. 5, with Bronze Age male means for tibial bending and torsional rigidity (J) and cross-sectional shape (I_{max}/I_{min}) exhibiting transitional values, and Iron Age and Medieval male means encompassing or falling below those of modern sedentary controls. Results by cemetery (in approximate chronological order) suggest that sedentism among Central European males may date back to the Late Bronze Age (~1300–800/750 BC) in this region, after which a shift

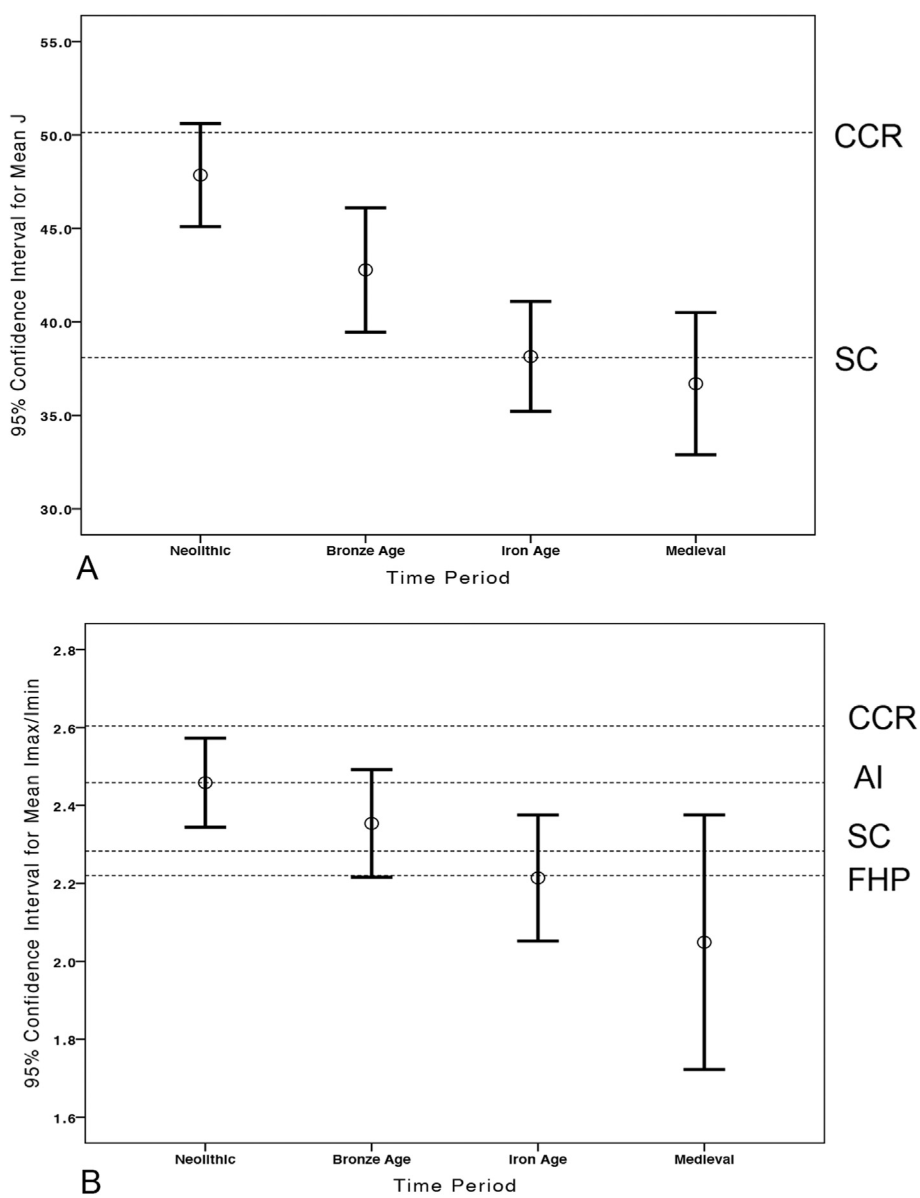

Fig. 5. Mean male tibial midshaft values and 95% confidence intervals for A) polar second moment of area (J) and B) shape in the maximum and minimum planes (I_{max}/I_{min}) relative to individuals of known sport and/or mobility pattern. Mean J in comparative samples: cross-country runners (CCR), 50.13; sedentary controls (SC), 38.10. Mean I_{max}/I_{min} in comparative samples: CCR, 2.605; Andaman Islanders (AI), 2.458; SC, 2.283; field hockey players (FHP), 2.22. All CCR, FHP, and SC means from Shaw and Stock (2009b), Table 2. All AI and FHP means from Stock and Pfeiffer (2001), Table 5. All means for J from Shaw and Stock (2009b) are size-standardized true values derived from CT images with visualization of the endosteal contour, so means would increase slightly if adjusted for %CA to approximate J in a solid section.

in tibial rigidity occurred to bring mean values down to those more typical of modern British sedentary individuals.

Though no comparative athlete sample is available for the females, all female tibial J and I_{max}/I_{min} values fall well below those of modern male sedentary controls (see Table 6 for female values). The great variety of tasks typically attributable to females, not only agricultural work but also a variety of crafts, such as pottery and textile production, and processing activities requiring the manipulative use of the dentition (Frayer, 2004; Lillie, 2008), likely produced less overall lower limb loading than that seen among males. However, it is also important to consider the impact of sex differences in relative levels of pubertal hormones, as these elicit differences in bone strength due to the surface-specific effects of testosterone and estrogen. Androgens promote structurally advantageous periosteal expansion (Seeman, 2003; Gosman et al., 2011), while estrogens induce endosteal bone packing (Garn, 1970, 1972; Libanati et al., 1999; Schoenau et al., 2001; Seeman, 2003; Gosman et al., 2011) that, although necessary for pregnancy, lactation, and/or menopause (Schoenau et al., 2001; Järvinen et al., 2003), does not confer as much structural integrity. Thus, additional factors in females may supersede the typical functional and energetic influences on bone mass and distribution to a certain extent (Järvinen et al., 2003).

The importance of pubertal sex hormones for the growth of mechanically strong bones also highlights another important consideration when interpreting behavior from adult skeletal remains. Because most bone deposition prior to puberty occurs at the mechanically relevant periosteal surface (Garn, 1970; Seeman, 2003; Gosman et al., 2011), loading at this time has more potent effects on limb bone cross-sectional properties and bone mineral density (Parfitt, 1994; Ruff et al., 1994, 2006; Kannus et al., 1995; Haapasalo et al., 1998, 2000; Bass et al., 2002; Kontulainen et al., 2002) than loading commenced after puberty. When loading is initiated after mid-adolescence, when endosteal apposition is more prominent, endosteally-derived increases in cortical bone density (Ruff et al., 1994; Trinkaus et al., 1994; Haapasalo et al., 1996, 1998, 2000; Bass et al., 2002; Kontulainen et al., 2002) play a larger role in the functional response to loading than does periosteal adaptation. Thus, temporal trends in lower limb loading in Central European males and females identified in the current study are likely reflecting in large part behaviors being performed during growth and early adolescence.

However, adult bone does retain some capability to adapt to loading in mechanically relevant ways (Kontulainen et al., 2002), and structurally competent bone morphology that is attained during the growth period will not be maintained into adulthood if adult loading patterns are not similar enough to prevent bone loss (Kriska et al., 1988; Greendale et al., 1995; Teegarden et al., 1996; Ruff et al., 2006). In addition, participation in adult behaviors likely begins to intensify in many preindustrial societies in conjunction with the adolescent growth spurt (Pearson and Lieberman, 2004; Ruff et al., 2006), and individuals in the late adolescent and early adult age groups are often well-represented in archaeological contexts and typically make up a large portion of the samples used in studies employing behavioral reconstruction (Ruff et al., 2006), as is the case in the current study. Thus, adult behaviors can reasonably be inferred from bone cross-sectional properties, and true adult behavior patterns in the current study were not likely drastically different than those being reflected in the skeletal remains.

Results of the current study also suggest a higher correspondence between biomechanical signatures of mobility and diaphyseal CSG in the tibia relative to the femur, a finding supported elsewhere in the literature (Stock, 2006). There was very little significant change in the femur through time, and though the pattern in male femoral I_x/I_y matched the pattern seen in tibial variables, the pattern in female TA and J did not. Plasticity in response to loading conditions is limited in femoral cross-sections, particularly of the proximal region (Ruff and Hayes, 1983; Trinkaus et al., 1998; Holt, 2003; Ruff, 2005a), by functional constraints imposed indirectly via locomotory (Ruff, 1991), climatic (Ruff, 1991, 1993, 1994; Stock, 2006; Cowgill et al., 2012), and obstetric (Ruff, 1987, 1995, 2005b) selection pressures acting on the breadth and shape of the pelvis. Tibial cross-sectional dimensions are not subject to functional constraint from body size/shape to the same extent, and exhibit poor predictive capacity for body mass in hominoids in general (Ruff, 2003). This is likely due in part to the role of the fibula in load bearing, which also demonstrates plasticity to locomotive characteristics among living hominoids and among athletes (Marchi and Shaw, 2011; Marchi et al., 2011).

Preliminary examinations of body size/shape in the Central European populations utilized in the current study will be expanded upon in future work, but mean stature and body mass tended to increase over time in both sexes, though only significantly so in females (unpublished data). In order to test whether or not patterns in femoral CSG properties were reflecting body size changes through time, femoral J and I_{max}/I_{min} extracted from the 75% section location (proximal femur) were compared temporally and tested for their correspondence with body size-related variables using Pearson's correlations (on raw unstandardized values of J; see Table 7 for summary statistics and statistical results). There was no significant temporal change in either J or I_{max}/I_{min} in the proximal femur among females or in I_{max}/I_{min} among males. However, male proximal femoral J increased through time, with significantly greater values in Medieval males than Neolithic males. This pattern is in direct opposition to the very strong temporal declines found in midshaft tibial J among the same males. In addition, when all males were pooled together, proximal femoral circularity (I_{max}/I_{min}) correlated significantly with both body mass and maximum femur length, though the proportion of variance in I_{max}/I_{min} accounted for by body size was very low. These results provide some preliminary evidence for the existence of a relationship between body size variables and cross-sectional dimensions in the proximal femoral diaphysis (75% section location) in Central European agricultural populations that warrants further investigation in future work.

4. Limitations

The possible influence of using solid section estimates of CSG properties on observed results must be considered. Most notably, as the endosteal contour was not considered, change in percent

Table 7
Summary statistics and significant results for male proximal femoral variables (75% of maximum length).

Group	N	J		I_{max}/I_{min}	
		Mean	SD	Mean	SD
Neolithic males	45	48.239	8.060	1.678	0.279
Bronze Age males	34	53.462	10.439	1.835	0.302
Iron Age males	18	52.502	10.091	1.741	0.321
Medieval males	11	**57.506**	9.613	1.567	0.223
Pooled time periods		J		I_{max}/I_{min}	
Correlation with:		p	r	p	r
Body mass		–	−0.089	<0.039	0.198
Maximum femur length		–	−0.138	<0.027	0.212

Bold indicates a significantly greater mean value in Medieval than Neolithic males ($p < 0.024$); dash indicates a lack of significance at $p < 0.05$ for Pearson's correlations.

cortical area [$\%CA = (CA/TA)^*100$] was not quantified or accounted for and could impact the significance of results. The midshaft location of femoral and tibial diaphyses exhibited low error rates between periosteally-derived CSG properties and true values in Macintosh et al. (2013). However, these error rates were quantified from only one population; the impact of using solid sections on estimates of true CSG properties and shape indices across multiple populations that may have different %*CA* is unknown. There is evidence from studies utilizing larger, more diverse samples that differences in %*CA* between populations appear to have minimal impact on population mean properties derived from external contours alone. In a geographically broad sample of humans from a variety of subsistence patterns, Stock and Shaw (2007) found that the removal of the endosteal contour had minimal effect on periosteal estimates of *TA* and *J*. Additionally, in a comparison of two human populations with the same *TA* but %*CA* at the opposite ends of the spectrum of normal human variation, mean *J* was minimally impacted (Sparacello and Pearson, 2010).

In addition, population discontinuities were not tested for in the current study. Thus, it is possible that genetic differences contributed somewhat to population differences in lower limb morphology. Though major population migrations are known from the Iron Age, including of Celts (Szabó, 1991; Kristiansen, 1998) and Scythians (Rolle, 1989; Zoffmann, 2000), neither Celts from Brno-Maloměřice nor Scythians from Tápiószele stand out when compared to the other Iron Age cemetery or to each other (Table 6; Fig. 4). The impact of population discontinuities may be mitigated somewhat by the fact that, relative to other cranial and postcranial morphology, the cross-sectional dimensions of long bone diaphyses are perhaps most highly plastic to environmental modification, demonstrating strong responsiveness to mechanical loading (e.g., Pearson, 2000; Welch et al., 2004; Ruff, 2008; Haapasalo et al., 2000; Blackburn, 2011). Some control over genetic differences between populations may be possible in future analyses with the incorporation of cranial geometric morphometric and non-metric dental data that were also collected on these populations.

5. Conclusion

Results documented diachronic change in lower limb bone morphology in both sexes across ~6150 years following the transition to agriculture in Central Europe (~5300 cal BC–850 AD) that was particularly pronounced in male tibiae. All male tibial CSG properties, as well femoral I_x/I_y, documented gradual but increasing sedentism through time, while temporal trends in female tibial shape ratios documented a similar though less pronounced decline. The introduction of major technological innovations in the Middle to Late Neolithic did not immediately alter lower limb loading in either sex, but pronounced Bronze Age sexual dimorphism suggests that technological and social change at this time may have altered gender relations and the division of labor by sex. The shift towards lower tibial rigidity and greater sedentism following the transition to agriculture likely occurred during the Late Bronze Age, though this was regionally variable across the Carpathian Basin. By the Early Iron Age, sexual dimorphism and lower limb loading were low in both sexes and remained there through the Early Medieval period, perhaps reflecting increasingly efficient methods of food production and high task specialization. These may have reduced overall lower limb loading and/or limited intensive loading to a smaller subset of the population. Overall, results documented systematic declines in lower limb loading and mobility among preindustrial Central Europeans subject to long-term cultural change following the transition to agriculture.

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